

Research Article

Spatial Distribution, Seasonal Dynamics, and Sex Ratio of *Lycorma delicatula* (Hemiptera: Fulgoridae) Adults on Tree of Heaven

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The spatial distribution and seasonal dynamics of the spotted lanternfly (*Lycorma delicatula*) on tree of heaven (*Ailanthus altissima*) were studied in Pennsylvania through weekly sampling of 30 trees (6 sites, 5 trees/site) from 27 July to 8 November 2020. Adults found on each tree were separated into six within-tree positions (lower trunk, middle trunk, upper trunk, first branch, second branch, and above second branch) by four directions (East, South, West, and North). In total, 78,796 adults were counted at the six study sites during the 15-week period. Significant differences in total adult count were found among trees, with a mean of 2,627 (254–12,023) adults/tree. Study site, tree diameter, and cardinal direction had no significant impact on adult spatial distribution. However, significantly more adults were found on the middle (1077), the lower (865), and the upper trunk (337) compared with the first (194), the second (93), and above second branches (60). Most adults were congregated on the lower and middle trunks. Seasonal dynamics followed adult development and migration patterns in the field, with peak populations observed in weeks 35 (24–30 August) and 37 (7–13 September) before declining. Female-based sex ratios ranged from 77.3 to 100% according to weekly monitoring of the lower 1 m trunk of 10 trees at 2 sites (5 trees/site) for 12 weeks from 17 August to 8 November, with 7,356 females and 197 males counted, respectively. Impact factors such as attack patterns, intraspecific congregation, adult seasonality, and sexual dimorphism in host selection are discussed.

1. Introduction

Biological invasion is the second most important threat to biodiversity globally after habitat destruction [1–4]. The successful introduction, establishment, and spread of invasive species in a new environment are the combined result of its behavior, attack pattern, host selection, resource utilization, seasonal development, population structure, intra- and interspecific competition, and other abiotic or biotic factors [5, 6]. Early detection and rapid response based on accurate information on invasion biology are crucial to the effective management of all invasive species [7]. Knowledge of the spatial and temporal distribution of the targeted pest is required for the construction of strategic responses in the management programs.

The spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae), an important pest of tree of heaven (*Ailanthus altissima* (Mill.) Swingle [Sapindales: Simaroubaceae]) from China [8], was first detected in Pennsylvania in 2014 [9, 10]. Current distribution of this pest in USA includes 13 states from Massachusetts in the east to Indiana in the midwest and North Carolina in the south [11]. As a polyphagous pest, it also feeds on grapevines (*Vitis* spp. [Vitales: Vitaceae]) and >100 other plant and tree species [10, 12, 13], posing a significant threat to the multibillion-dollar fruit, nursery, landscape, and hardwood industries in the United States [14, 15].

Lycorma delicatula adult emergence starts in late July in Pennsylvania [13, 16, 17]. Newly emerged adults are pink (body and wing pads) with black compound eyes, yellow antennae, yellow vertex, and light-colored legs (Figure 1(a)).

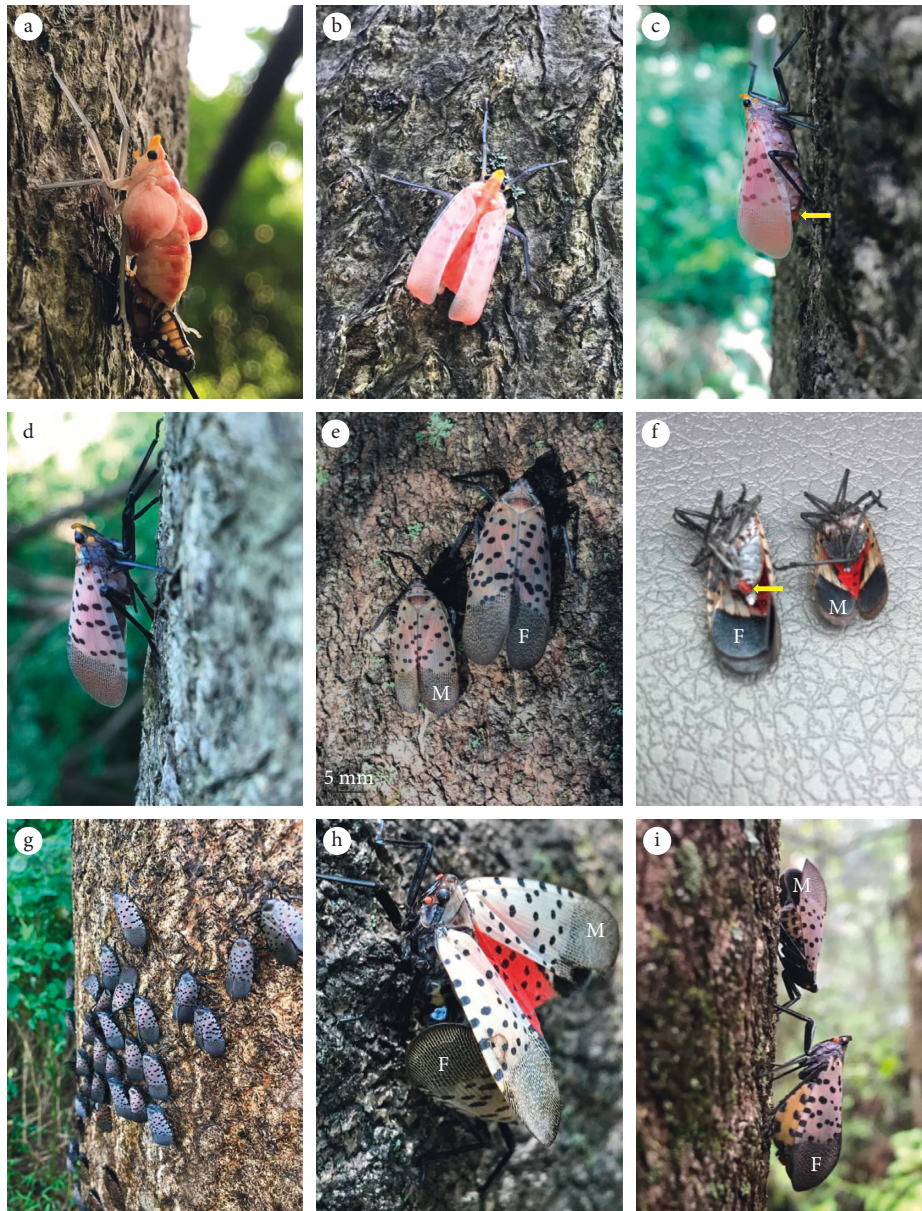


FIGURE 1: *Lycorma delicatula* adult development in the field. (a) An emerging adult with pink body, black compound eyes, yellow antennae and vertex, light-colored legs, and pink wing pads. (b) A newly emerged adult with expanding wings and black legs. (c) A full-fledged female with pinkish body and wings. (d) A fully sclerotized adult with darkening body and vertex. (e) Male versus female—dorsal view. (f) Female versus male—ventral view. (g) Multiple adults aggregating on trunk of tree of heaven. (h) A mating pair. (i) Mature male versus gravid female. Yellow arrows in (c) and (f) indicate red valvifers on female abdomen. M—male, F—female.

Within a few hours after emergence, wing pads begin to expand to show venation and gray spots on the surface (Figure 1(b)). Full-fledged adults (Figure 1(c)) are mostly pink with black legs. Complete body sclerotization (Figure 1(d)) usually finishes within 48 hours. Adults are 14–17 mm long with a wingspan of 40–45 mm for males and 18–22 mm long with a wingspan of 50–52 mm for females (Figure 1(e)) [8]. Females can be separated from males by the presence of the red valvifers (Figures 1(c) and 1(f)) at the end of the abdomen [10]. After several weeks of intensive feeding in aggregation (Figure 1(g)), mating (Figure 1(h)) occurs between early September and late October

[16, 18, 19]. Both males and unmated females are equally capable of taking the long-distance (10–50 m) flights, while mated females are limited to short-distance (<4 m) dispersals [18, 20, 21]. Mature males and gravid females have expanded abdomens with larger yellow areas (Figure 2(i)) [19] compared with early-stage adults (Figure 2(f)). Gravid females begin to lay eggs in mid-September until early November [13, 16–18]. Most adults die by early to mid-November when ground temperature falls below zero [13, 17].

The spatial distribution of *L. delicatula* adults on grapevines has been studied by Leach and Leach [22].

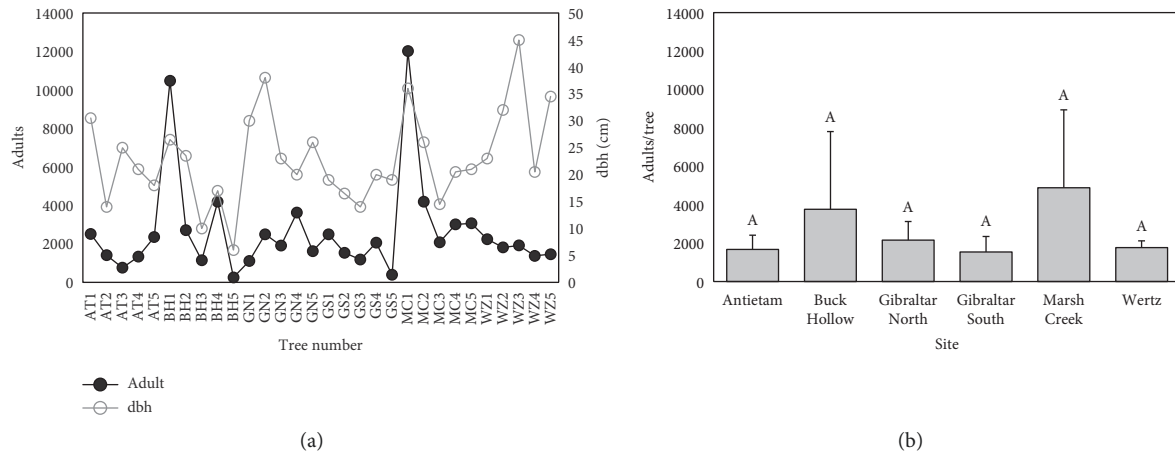


FIGURE 2: *Lycorma delicatula* adult count (a) total by tree and (b) average (mean \pm SD) by site. AT: Antietam, BH: Buck Hollow, GN: Gibraltar North, GS: Gibraltar South, MC: Marsh Creek, WZ: Wertz. Means in (b) followed by the same uppercase letter are not significantly different ($\alpha = 0.05$).

However, no similar comprehensive studies have been carried out on tree of heaven despite being the primary host for its nymphs and adults [13, 17, 23, 24]. On the other hand, adult seasonal development on tree of heaven has been monitored on the lower 2 m trunk [17], and sex ratio has been documented in the field as part of studies on its behavior (e.g., [18, 25]), trapping (e.g., [26, 27]), or late-season host selection [28]. Our null hypothesis is that *L. delicatula* adult population is randomly distributed on tree of heaven with unbiased sex ratio and normal seasonality. The objectives of this study were therefore to (1) understand the spatial distribution of *L. delicatula* adults on tree of heaven, (2) monitor the seasonal dynamics of its field populations, and (3) examine its sex ratio based on adults on the lower 1 m trunk.

2. Materials and Methods

2.1. Study Sites. This study was carried out at six mixed hardwood sites (0.5–1.0 ha) (Antietam, Buck Hollow, Gibraltar North, Gibraltar South, Marsh Creek, and Wertz) in southeastern Pennsylvania in 2020. See the work of Liu and Hunter [29] for site location, stand condition, infestation history, chemical control of *L. delicatula*, and herbicide treatment of tree of heaven at each site. Nolde Forest was excluded from this study due to complete tree mortality of tree of heaven associated with *L. delicatula* feeding damage at the site in the spring of 2020.

2.2. Sample Trees. Five healthy trees of heaven free of entanglement from vines were randomly selected near the epicenter of the infestation from each site for this study. Trees ranged from 3.5 to 9.0 m in height and from 6.0 to 45.0 cm in diameter at breast height (dbh). Efforts were made to select trees at least 5 m apart from each other at each site to prevent potential overlapping of crowns.

2.3. Spatial Distribution. To study the spatial distribution of *L. delicatula* adults on tree of heaven, all sample trees were visually monitored weekly from 27 July to 8 November 2020. The trunk and the entire crown of each tree were divided into four equal quadrants based on cardinal directions (East, South, West, and North) before inspection. Branches in the crown were separated into respective quadrants based on their origins along the bole. Within each cardinal direction, the tree was further divided to six within-tree positions: lower trunk (<2 m), middle trunk (2 m to the first branch), upper trunk (above the first branch), the first branch (first-order branches), the second branch (second-order branches), and the above second branch (third- and above-order branches). Trunk and branch surfaces were then visually searched for *L. delicatula* adults at two observing distances. Adults on the lower and middle trunks were easily spotted with unaided eyes by standing at 0.5 m from the base of the tree, whereas those on the upper trunk and the branches were observed 4 m away with the help of a pair of Nikon Action EX 8 \times 40CF binoculars (Nikon Vision Co., Ltd., Tokyo, Japan). Results of preliminary observations showed that these were ideal distances to examine the entire tree. Equal observing distance from the base of the tree was needed to protect the same field of view (FOV) from all directions. Only fully visible adults in the FOV were counted to preclude potential double-counting. The same procedure was repeated from each cardinal direction for every tree at each site. Surveys usually took place in the early mornings for optimal viewing conditions. Days with heavy rains or strong winds were generally avoided to prevent potential weather interference.

2.4. Seasonal Dynamics. Seasonal dynamics of *L. delicatula* adults on tree of heaven were monitored weekly from 27 July (week 31) to 8 November (week 45) by counting the adults on each tree. The total number of adults found on each tree

was recorded. Weekly population was analyzed by within-tree positions and study sites. Population trend was examined in the context of adult development and migration patterns in the field.

2.5. Sex Ratio. To study the sex ratio of *L. delicatula* adults on tree of heaven, the lower 1 m trunk of 10 sample trees (two sites—Buck Hollow and Marsh Creek, 5 trees/site) was examined weekly from 17 August (week 34) to 8 November (week 45). Adults were sexed by size difference first (Figures 1(e) and 1(f)) before confirmation by presence/absence of the red valvifers (Figures 1(c) and 1(f)). For those individuals in tight clusters or on trunks too close to the ground where side view position was difficult to obtain, a gentle lift of the wing tips from behind with a small twig was enough to expose the red valvifers for females. The total numbers of males and females were recorded each week by tree.

2.6. Data Analysis. A linear model was used to fit total adults observed on each tree with its diameter. Mean adult count per tree was subjected to Shapiro-Wilk normality test before analysis. If data were not normally distributed, Kruskal-Wallis test was used in the one-way ANOVA (analysis of variance) to detect the effect of tree, study site, cardinal direction, and within-tree position. Significant effects by ANOVA were followed by pairwise Wilcoxon rank-sum test with a *P* value adjusted by Benjamini-Hochberg method. Chi square test on count data was used to detect differences in total adult count between trunk and branch, as well as females and males. Stepwise regression models were used to fit adult count on each within-tree position with the total adult count on the tree. Friedman test with repeated measures was used to detect time effect in adult population dynamics and sex ratio during the season [30].

3. Results

3.1. Total Adult Count. In total, 78,796 adults were counted at the six study sites during the 15-week (once/week) observation period, including 8,367 at Antietam, 18,786 at Buck Hollow, 10,767 at Gibraltar North, 7,673 at Gibraltar South, 24,384 at Marsh Creek, and 8,819 at Wertz. Adult count differed significantly ($\chi^2 = 100.14$, $df = 28$, $P < 0.001$) among trees, with a mean of 2,627 (254–12,023) adults/tree (Figure 2(a)). Adult count on tree MC1 was significantly higher than those on trees AT2, AT3, AT4, BH3, BH5, GN1, GN3, GN5, GS2, GS3, GS5, WZ2, WZ4, and WZ5. Significant difference in adult count was also found between trees BH1 and BH5, MC2 and BH5, and MC2 and GS5. Trees BH2 and GS5 died by week 36 (August 31–September 6). No positive correlation was detected between adult count and tree diameter ($F = 3.069$, $df = 1, 28$, $P = 0.091$). Adult count on small trees (e.g., BH3 and BH5) was generally low; however, low numbers were also found on medium-sized trees (e.g., AT3 and GS5). The number of adults per tree generally ranged from 1,000 to 4,000, while extremely high numbers were observed on trees MC1 and BH1 (Figure 2(a)).

No significant difference in adult count was found among different study sites ($\chi^2 = 8.239$, $df = 5$, $P = 0.144$) despite relatively higher numbers at Marsh Creek and Buck Hollow (Figure 2(b)). The lowest number was found at Gibraltar South (Figure 2(b)). Dead sample trees at Buck Hollow and Gibraltar South in the middle of the season might have negatively impacted adult counts at those sites.

3.2. Cardinal Direction. No significant difference in mean adult count was found among cardinal directions ($\chi^2 = 0.332$, $df = 3$, $P = 0.954$). More adults were found on the south side. A relatively higher number was also found on the east side compared with that on the north side. The lowest number was found on the west side (Figure 3(a)).

3.3. Within-Tree Position. Significant differences in mean adult count were found among within-tree positions ($\chi^2 = 113.97$, $df = 5$, $P < 0.001$), with significantly higher numbers found on the middle and the lower trunks ($P < 0.05$) (Figure 3(b)). Mean adult count on the upper trunk was significantly lower than those on the middle and lower trunks, but it was higher than those on all three branch positions ($P < 0.05$) (Figure 3(b)). No significant difference in mean adult count was found among branch positions (Figure 3(b)).

Significantly more adults were found on trunks than on branches ($\chi^2 = 5,527.400$, $df = 5$, $P < 0.001$), with 68,377 adults counted on the lower, middle, and upper trunks compared with 10,419 adults on the first, second, and above second branches throughout the season. Weekly proportion of adults on trunk sections combined ranged from 57.1% in week 31 (27 July–2 August) to 93.4% in week 43 (19–25 October) (Figure 4(a)). Adult proportion on each trunk position also varied between observation weeks, ranging from 15.3% in week 31 to 42.9% in week 37 (7–13 September) on the lower trunk, from 15.3% in week 31 to 56.0% in week 44 (26 October–1 November) on the middle trunk, and from 9.2% in week 35 (24–30 August) to 26.5% in week 31 on the upper trunk, respectively (Figure 4(a)). Adults on branches accounted for <20% of the weekly total counts during the observation period except in weeks 31, 34 (17–23 August), and 45 (2–8 November) when 42.9, 21.0, and 20.6% of adults were found on branches, respectively (Figure 4(a)). Adult proportion ranged from 3.8% in week 43 to 31.2% in week 31 on the first branch, from 2.0% in week 43 to 6.6% in week 34 on the second branch, and from 0.8% in week 43 to 5.3% in week 31 on the above second branch, respectively (Figure 4(a)).

While adult count stayed relatively stable on the upper trunk, the first, the second, and the above second branches except at the beginning or the end of the season, adult count on the lower and middle trunks followed the same trend as the total adult count of the tree (Figure 4(b)). It increased from week 31 to week 35, slightly decreased in week 36 (31 August–6 September), and rebounded a week later before decreasing significantly toward week 39 (21–27 September) and the end of the season (Figure 4(b)). Results of stepwise regression analysis showed that the total adult count on each

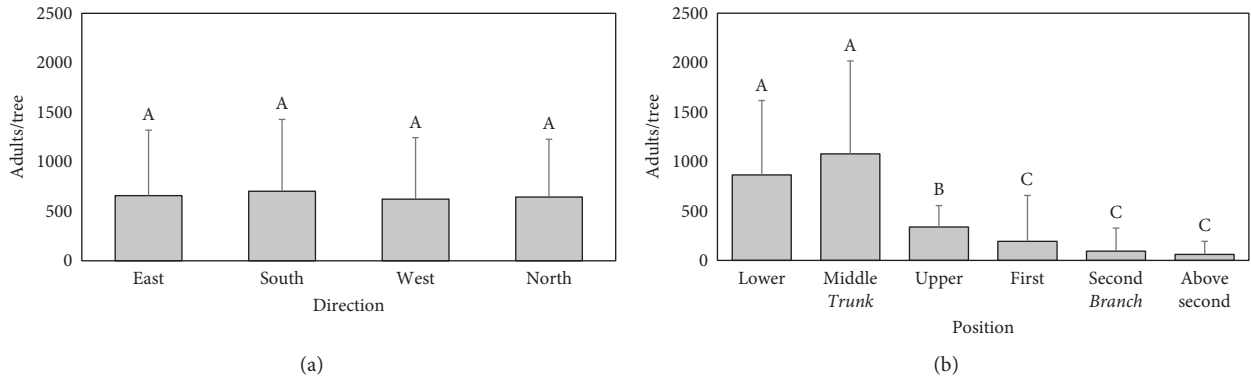


FIGURE 3: *Lycorma delicatula* adult count (mean \pm SD) by (a) direction and (b) within-tree position. Means followed by the same uppercase letter are not significantly different ($\alpha = 0.05$).

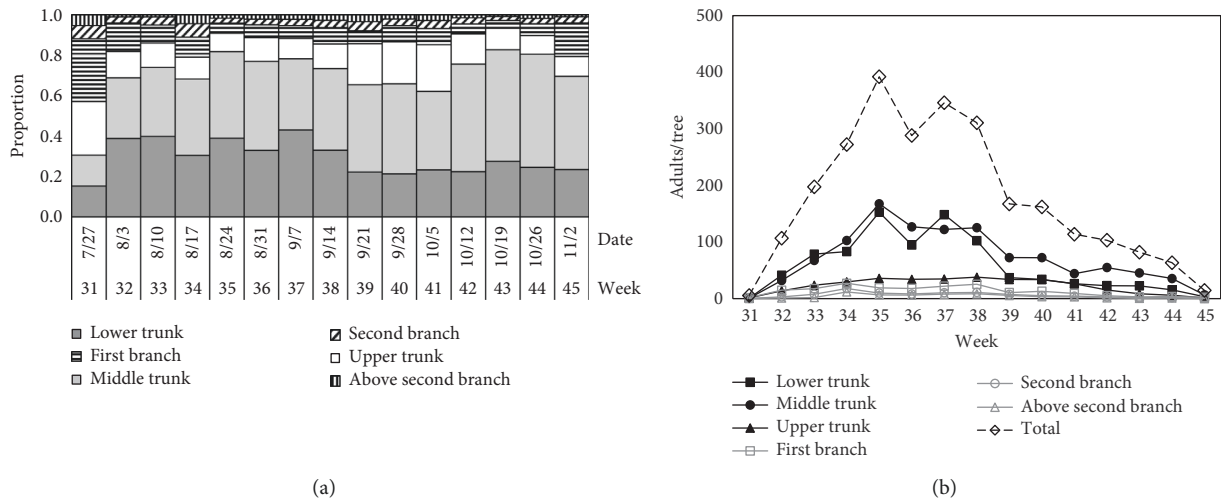


FIGURE 4: Seasonal composition of *Lycorma delicatula* adult at different within-tree positions (a) by proportion and (b) by mean (\pm SD) count.

tree (Y) could be accurately predicted by those found on the lower trunk (X_1) and the middle trunk (X_2) using formula $Y = -333.56 + 2.32X_1 + 0.89X_2$ ($R^2 = 0.974$, $P < 0.001$) with significant intercept and coefficient.

3.4. Seasonal Dynamics. *Lycorma delicatula* adults were first observed on tree of heaven at Marsh Creek, followed by Gibraltar South, Gibraltar North, Buck Hollow, Antietam, and Wertz. In general, adult population increased in a straight line from week 31 to reach peak in week 35, took a small dip in week 36, bounced back to the second peak in week 37, and remained at similar level in week 38 (14–20 September) before significantly decreasing toward the end of the season (Figure 4(b)). Seasonal dynamics of *L. delicatula* adults on tree of heaven differed among study sites. Significant effect on observation time (week) was detected at Antietam ($\chi^2 = 53.186$, $df = 14$, $P < 0.001$) and Wertz ($\chi^2 = 58.624$, $df = 14$, $P < 0.001$). No adults were recorded in week 31 at those two sites. Population increased from week 32 (3–9 August) to reach the peak in week

36 (Wertz) or week 37 (Antietam) before gradually decreasing toward the end of the season. A small increase in adult population was also found in week 40 (28 September–4 October) at both sites (Figure 5). Adult population at Buck Hollow followed a trend similar to that of Antietam and Wertz, with significant time effect observed ($\chi^2 = 60.810$, $df = 14$, $P < 0.001$). However, it differed from them by having larger variations among trees and an earlier peak population in week 35. As a result, postpeak population increase was also observed three weeks earlier. No small increase in adult population was found beyond week 35 (Figure 5). Significant time effect was also found at Gibraltar North ($\chi^2 = 60.758$, $df = 14$, $P < 0.001$) and Gibraltar South ($\chi^2 = 52.300$, $df = 14$, $P < 0.001$). However, adult population peaked in week 35 and stayed relatively stable for the next three weeks before decreasing in weeks 39 and 40 (Figure 5). Small increases in weeks 41 (12–18 October) and 42 (19–25 October) were recorded for Gibraltar South and Gibraltar North, respectively (Figure 5). The population trend at Marsh Creek was more variable than any other sites, with multiple peaks in weeks 33 (10–16 August), 35, 37, and 40,

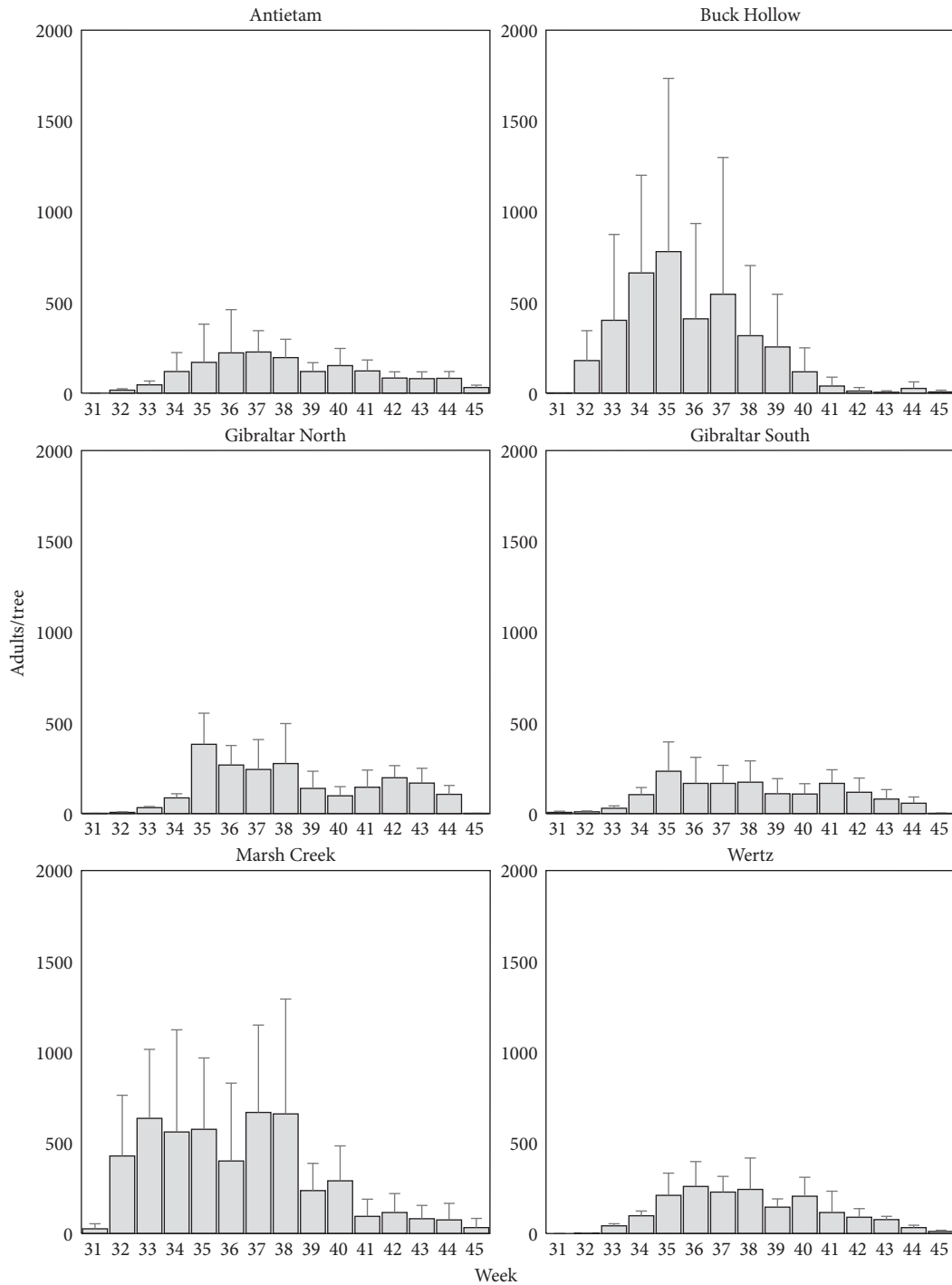


FIGURE 5: Seasonal dynamics of *Lycorma delicatula* adult count at different study sites.

respectively (Figure 5). Significant increase in adult population was observed between weeks 31 and 32 with much lower population levels from week 40 toward the end of the season. Significant time effect was also found at this site ($\chi^2 = 64.358$, $df = 14$, $P < 0.001$).

3.5. Sex Ratio. Significantly more females than males were found on the examined portions of trees of heaven ($\chi^2 = 35.737$, $df = 1$, $P < 0.001$), with 7,356 females and 197

males counted on the lower 1 m trunk for the entire observation period. Significant effect on observation time (week) was found for females ($\chi^2 = 20.247$, $df = 11$, $P = 0.042$) but not for males ($\chi^2 = 14.946$, $df = 11$, $P = 0.184$). Female-based sex ratio ranged from 77.3 to 100% during the season (Figure 6(a)). It increased from 95.1% in week 34 to 99.0% in week 37 before decreasing to 77.3% in week 44. No males were recorded in weeks 42 and 45, which resulted in a sex ratio of 100% of females for both weeks.

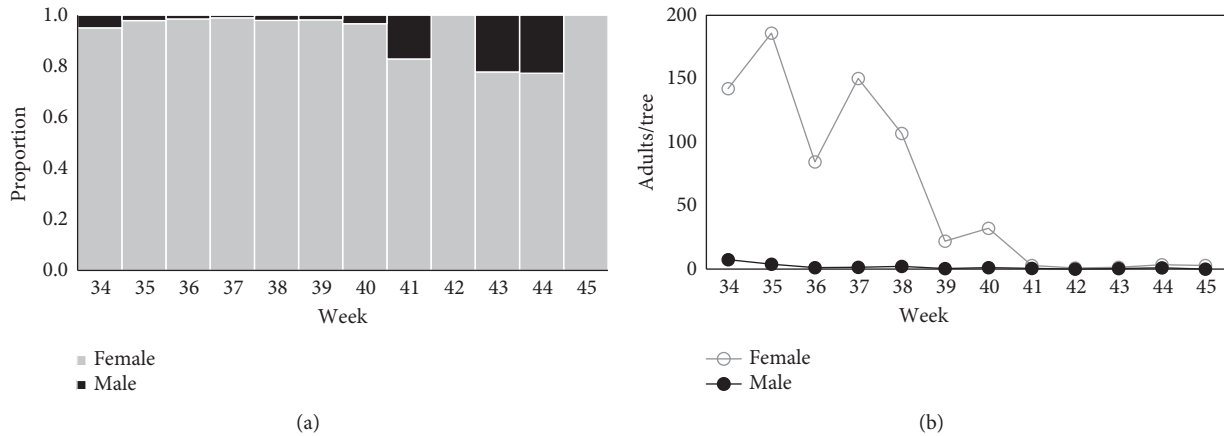


FIGURE 6: Seasonal sex ratio of *Lycorma delicatula* (a) by proportion and (b) by count.

Mean female count followed a similar trend with total adult count, which peaked in week 35 and dipped in week 36 before bouncing back in week 37 and significantly decreased in week 39 (Figures 4(b) and 6(b)). On the other hand, mean male count stayed flat during the entire observation period, with relatively higher numbers found in weeks 34, 35, and 38 (Figure 6(b)).

4. Discussion

Contrary to our null hypothesis, the spatial distribution of *L. delicatula* on tree of heaven was not random, with some trees at certain sites attracting more adults than others. Total adults recorded on trees MC1 and BH1 (medium-sized healthy trees at the border of the site) were at least four times higher than the site mean, accounting for 55.8 and 49.3% of the total adults observed at each site, respectively (Figure 2(a)). Tree diameter did not have significant effect on total adults recorded on each tree (Figure 2(a)) nor did the study site (Figure 2(b)). Francese et al. [26] caught significantly more adults on trees of heaven along woodland edges than those in the open field. However, comparison between individual trees was not attempted in their study. Strong edge effect was also found in vineyards when 54% of adults were caught on grapes within 15 m from the border [22], while adult fidelity to certain maple (*Acer* spp.) trees was confirmed late in the season [28]. Variation in attack patterns is commonly found in other insect species. Bark beetles are known for their mass attacks on weakened or dying trees during the initial infestation stage [31], whereas emerald ash borer (*Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae)) preferred stressed trees [32]. More research is needed to determine whether weakened or stressed tree of heaven or maple trees are more attractive to *L. delicatula* adults. Tree location, health condition, attack patterns, and infestation history may have influenced host selection for adults.

Within-tree position, rather than tree diameter or cardinal direction, significantly affected adult count on the trees (Figures 2(a), 3(a), and 3(b)). The majority of the adults were congregated on the lower and middle trunks throughout the season (Figure 4(a)). Negative correlation between insect

density and height-above-ground and directional preference has been observed in woodboring insects as tree diameter, bark thickness, nutrient contents, and temperature all played a role in their respective vertical and cardinal distributions (e.g., [33–35]). However, similar influences from those factors may not be expected for *L. delicatula* as both nymphs and adults can move freely in any direction along the trunk and between trees. The intraspecific aggregation of adults observed in this study is probably more related to mating and breeding than foraging as adequate trunk space is generally available even on trees with high population density (Liu, personal observation). Prior to the introduction of *L. delicatula*, ailanthus webworm (*Atteva aurea* (Fitch) [Lepidoptera: Attevidae] = *Atteva punctella* (Crammer) [Lepidoptera: Yponomeutidae]) was the only common native pest on tree of heaven in North America [36, 37]. Distribution of the introduced ailanthus silkmoth (*Samia cynthia* (Drury) [Lepidoptera: Saturniidae]) is spotty along the Atlantic coast from Connecticut to Georgia and west to northern Kentucky [38, 39]. Both pests feed on leaves and are rarely encountered in Pennsylvania. However, tree of heaven is very abundant in the eastern United States [40]. Therefore host selection for *L. delicatula* is very unlikely driven by host scarcity or interspecific competition. Potential aggregation mechanisms (e.g., pheromone and substrate borne vibration) will need to be investigated.

Seasonal dynamics of *L. delicatula* adults on tree of heaven generally followed the temporal and migration patterns as reported before. After completing early nymphal development on various hosts including tree of heaven, the 4th instar nymphs and adults started to congregate on tree of heaven for nutrient acquisition and defense sequestration [13, 41]. As a result, adult population peaked on this host between mid-August and late August (Figures 4(b) and 5). Population decreased temporarily from the peak levels after that, probably due to migration to nearby alternative hosts by a portion of the adults. Aggregation toward tree of heaven continued in the next couple of weeks, resulting in a second peak between early and mid-September (Figures 4(b) and 5). Adult population declined significantly after that due to the long-distance

flights (males and unmated females) and short-distance dispersals (males and mated females) to alternative hosts in early October [17, 28]. The small increase between late September and mid-October (Figures 4(b) and 5) could be the result of reverse migration by gravid females for oviposition as tree of heaven is one of the preferred substrates [13, 29]. Information on adult movement between and within hosts during the season is needed.

Lycorma delicatula adult sex ratio recorded on tree of heaven was extremely female-biased, with very few males observed from late August to early November (Figures 6(a) and 6(b)). Similar ratios (>80%) were also reported by Francese et al. [26] between late September and late October despite having more males caught at the beginning of the adult stage (late July to early August) when field populations were still dominated by the 4th instar nymphs. Close to 50% sex ratios were routinely recorded on tree of heaven trunks and branches throughout the season, with only a couple of instances in early August [18]. On the other hand, Nixon et al. [27] reported male-biased sex ratios between mid-September and late October and female-biased sex ratios toward the end of the season. Male-biased sex ratios were also reported in South Korea between late September and early October [42]. Difference in sampling methodology may help explain the discrepancies between studies. Visual inspection on a portion of the trees (0–2 m trunk) was used in this study and in Baker et al.'s study [18], while trapping with brown sticky bands or various cages was utilized in other studies [26, 27, 42]. It has been suggested that tree species and tree size might have played a role in the sexual dimorphism in host selection as larger (>15 cm) trees of heaven harbored almost exclusively females, while males were commonly found on small-diameter tree of heaven and other hosts such as grapes (*Vitis* spp.) and black willow (*Salix nigra*) [25]. No such distinction between sexes was observed for tree of heaven in this study as male counts were constantly lower on both large and small trees. Sex ratio was male-biased from late August to early October and female-biased afterwards on maple trees because males migrate/disperse earlier than females [28]. Total sampling of all hosts at the entire site throughout the season is needed for the full picture of the sex ratio dynamics in the field.

The relationship between adult and egg mass spatial distribution on tree of heaven may also deserve more attention as most adults were congregated on lower and middle trunks, while most egg masses were found on the upper trunk and first order branches [29, 43, 44]. Gravid females must disperse within or between trees to avoid interspecific competition during oviposition. Newly hatched nymphs from egg masses in the canopy may have the advantage of landing on diverse hosts when dislodged [45]. New studies using real-time tracking of adults could provide answers to this kind of questions.

Results from this study showed the importance of tree of heaven in the population dynamics of *L. delicatula* in the field in eastern North America. Spatial distribution and seasonality as a result of late-season movement to other hosts such as black birch (*Betula lenta* L. [Fagales:

Betulaceae]), red maple (*Acer rubrum* L. [Sapindales: Sapindaceae]), and silver maple (*Acer saccharinum* L. [Sapindales: Sapindaceae]) [17, 28] should also be considered. However, for better results, monitoring and management effort should concentrate on tree of heaven between mid-August and late August before adult mating and migration as this species remains the focal point of most field infestations.

Data Availability

The data that support the findings of this study are openly available at Zenodo: <https://doi.org/10.5281/zenodo.5949360>.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Authors' Contributions

HL designed the experiment, conducted field work, completed data analysis, and wrote, read, and approved the manuscript. MH conducted field work and approved the manuscript.

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